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ORIGINAL PAPER

Conquerors or exiles? Impact of interference competition among invasive Ponto-Caspian gammarideans on their dispersal rates

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Abstract Ponto-Caspian gammarids have invaded European waters, affecting local communities by predation and competition. Their ranges and dispersal rates vary across Europe, which may result from their interspecific interactions, accelerating or reducing migrations. We checked this hypothesis by testing interference competition among co-occurring invaders: *Dikerogammarus villosus*, *D. haemobaphes* and *Pontogammarus robustoides*. We used 140-cm long tanks (gravel substratum), divided into seven compartments. We introduced 25 "residents" into the outermost compartment, separated with a barrier. After 1 h, we introduced 25 "intruders". After the next 1 h, we removed the barrier and the gammarids dispersed in the tank. After 4 or 20 h, we counted the gammarids in the compartments. We tested all pairwise species combinations and single-species controls. *Dikerogammarus villosus* displaced other species (*P. robustoides* only after 4 h) and reduced its own motility after 20 h in their presence. *Pontogammarus robustoides* stimulated the short-time migrations of *D. villosus* intruders and of *D. haemobaphes*. As *P. robustoides* migrated spontaneously much more than *Dikerogammarus* spp., its impact decreased after longer time. *Dikerogammarus haemobaphes* stimulated the short-time movement of *P. robustoides* intruders but reduced the long-time relocation of this species. In general, gammarid dispersal increased in the presence of stronger competitors (*D. villosus* and *P. robustoides*, especially residents) and decreased in response to weaker competitors (*D. haemobaphes*). Thus, competitive interactions may affect dispersal of invasive gammarids and contribute to the fastest spread of the weakest competitor, *D. haemobaphes* observed in the field, whereas the strongest species, *D. villosus* was the latest newcomer in many novel areas.

Keywords *Dikerogammarus* · *Pontogammarus* · Spatial partitioning · Species displacement · Migrations · Invasion potential

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Introduction

Spatial distribution and co-occurrence of species at the microhabitat scale is a result of intra- and interspecific interactions (Waser 1985). The closer related species and the more their ecological niches overlap, the more competitive interactions can be expected, and their co-existence at the long time scale is suggested to be impossible even if a short time co-occurrence has been observed (Chase and Leibold 2003; Snyder and

Chesson 2003). Individuals compete for the same resources which may be categorized as food or space including shelters against predators. Interference competition is observed when animals actively defend their inhabited territory including aggressive behaviour leading to injuries of the competitors (Schoener 1983). A specific type of this interaction is an intraguild predation (IGP) in which competitors representing the same guild prey on each other (Polis et al. 1989). It is known that asymmetrical IGP, when one of the species preys more efficiently on the other, strongly influences habitat selection by species in an ecosystem (Heithaus 2001). The stronger competitor and/or predator makes the weaker one to leave preferable habitats and shift to less favourable ones (e.g. Otsuki and Yano 2014). The outcompeted individuals increase their activity, even facing the risk of being preyed by a top predator or not finding an alternative suitable space to live (e.g. Shurin and Allen 2001). If the fragile species is not successful in finding a new territory, its population may decline, but in heterogeneous environments such interaction usually results in spatial partitioning of habitats by the species (reviewed in Amarasekare 2003). This avoidance of unfavourable conditions, including competition and/or predation is one of the main drivers of species dispersal (e.g. Ronce 2007). Thus, considering the above, one may expect the weaker competitor exhibits a higher dispersal rate. On the other hand, several studies showed that individuals in worse physiological condition started their density or food dependent dispersal later and moved over shorter distances than strong, healthy (thus more competitive) individuals (e.g. Bonte and de la Pena 2009; Delgado et al. 2010).

Biological invasions, which are nowadays one of the major threats to global biodiversity (e.g. Lambertini et al. 2011), are one of the greatest opportunities to study mechanisms and consequences of species dispersal (e.g. Van Riel et al. 2007, 2011). The invasive freshwater amphipods may serve as a model group for such studies. Several amphipod species with relatively similar ecological niches successfully spread into European waters (Bij de Vaate et al. 2002; Grabowski et al. 2007b). They did not colonize the same water bodies at the same time, and a sequence of invasions of particular species can be observed (e.g. Holdich and Pöckl 2007; Grabowski et al. 2007b). In most cases the newcomer significantly moderated the community structure (e.g. Dick and Platvoet 2000; Jażdżewski et al. 2004; Krisp and Maier 2005; Kinzler et al. 2009; Chen et al. 2012; Truhlar and Aldridge 2015). In addition, several field studies showed spatial segregation of gammarid species, suggesting a habitat shift in the presence of related species (Kley and Maier 2005; MacNeil and Platvoet 2005; Hesselschwerdt et al. 2008; Żytkowicz and Kobak 2008; Platvoet et al. 2009; own unpublished data). Also experimental studies confirmed increasing swimming activity and movement of a "weaker" species (e.g. *Gammarus pulex*, *G. tigrinus* and *Pontogammarus robustoides*) to a different substratum in the presence of a stronger gammarid competitor (here *Dikerogammarus villosus*) (Van Riel et al. 2007; Platvoet et al. 2009; Jermacz et al. 2015a). These outcompeted taxa were also observed more often in a drift (Van Riel et al. 2011) or penetrating waters still not invaded by the other species, going upstream the river or entering affluents (Kley and Maier 2006), which might suggest their higher affinity for dispersal.

The influence of interference interactions on dispersal abilities of invasive amphipods has not been studied experimentally. We focused our study on three Ponto-Caspian gammarids (*Dikerogammarus haemobaphes*, *D. villosus* and *Pontogammarus robustoides*) which are widely distributed in Europe and their introduction has led to drastic changes in the macroinvertebrate community in colonized waters (Dick and Platvoet 2000; Arbaciauskas 2002; Jażdżewski et al. 2002, 2004; Berezina and Panov 2003). They are relatively large compared to native gammarids (Grabowski et al. 2007a) and exhibit several biological traits promoting their invasion, such as high reproductive abilities (reviewed in Grabowski et al. 2007a), opportunistic diet with effective predation (Platvoet et al. 2009; Bącela-Spychalska and Van der Velde 2013) as well as wide tolerance to ecological parameters (summarised in Bącela and Konopacka 2005; Rewicz et al. 2014; Bącela-Spychalska 2015).

Despite the fact that these species show slightly different preferences for hydrological conditions (Dedju 1980), they co-occur in many water bodies or were in contact in the past in native and invaded range (Carausu et al. 1955; Dedju 1980; Jażdżewski et al. 2004; Berezina 2007; Leuven et al. 2009). Although all the species could colonize new areas via similar routes (Bij de Vaate et al. 2002; Leuven et al. 2009),

they did not start to spread and establish at the same time. *Dikerogammarus haemobaphes*, which was the first *Dikerogammarus* species expanding its range via all possible migration corridors (Jażdżewski 1980), after its successful establishment faced the subsequent invasion of *D. villosus* in many European rivers: the Danube, Rhine, Oder and Vistula. The latter species outnumbered its congener very efficiently in most of these waters (Kley and Maier 2003; Müller and Hertel 2004; own unpublished data). On contrary, in the UK, *D. villosus* was recorded first (2010) and *D. haemobaphes* was notified in two year time (Environment Agency 2012). Interestingly, in this case *D. haemobaphes* is more widespread and seems to be more successful (Environment Agency 2012; 2013). *Pontogammarus robustoides*, which is very abundant in dam reservoirs, lagoons and lentic sections of rivers, e.g. the Vistula and Oder, cohabits many sites with the two *Dikerogammarus* species (Bącela and Konopacka 2005; Żytkowicz et al. 2008; own unpublished data). All three gammarids, specifically adults, in experimental studies have exhibited similar, strong preferences for stony habitats (Devin et al. 2003; Van Riel et al. 2009; Boets et al. 2010; Jermacz et al. 2015b). Thus, in the case of co-occurrence, they are likely to interact strongly with one another.

In this study we intended to check if variable dispersal rates and sequences of appearance of particular invasive Ponto-Caspian gammarid species in different parts of Europe depend on their reciprocal interspecific interactions at localities in which they co-occur. We hypothesized that weaker species would increase their dispersal rate after the introduction of a stronger competitor, particularly *D. villosus*, the largest species among them (Rewicz et al. 2014). On the other hand, the presence of related species of similar ecological demands may also indicate the suitability of a given location and result in the decrease of dispersal, particularly of stronger competitors. It is known that an individual occupying a territory (resident) is more likely to win an interference competition than an intruder, trying to seize it (Grafen 1987; Jennions and Blackwell 1996). Thus, we also hypothesized that the outcome of the interaction between gammarid species would depend on the sequence of their introductions to the environment, with the newcomer being less likely to establish at a cohabited site and moving further.

Materials and methods

Animals

We collected *Dikerogammarus villosus* and *Pontogammarus robustoides* individuals from the Włocławek Reservoir (the lower River Vistula, Central Poland), N 52°37′03″, E 19°19′37″ and *D. haemobaphes* from the Lucieńskie Lake, N52°29′46″, E 19°26′44″. In the laboratory, we placed them in stock tanks (temperature 19–22 °C) with aerated and filtered water and fed daily with frozen chironomid larvae and commercial fish food pellets. They were used in experiments 1–4 weeks after collection. We assessed gammarid sizes with ImageJ 1.40 g software (W.S. Rasband, U.S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/i), using photographs of 100 randomly selected individuals from each species. Mean body length ± SD of the studied individuals was 14.2 ± 2.2 mm (*D. villosus*), 13.4 ± 2.6 mm (*P. robustoides*) and 11.8 ± 2.9 mm (*D. haemobaphes*), reflecting natural differences in body size between the species (Grabowski et al. 2007a).

Experimental setup

We conducted experiments in glass tanks 140 cm long and 15 cm wide, with the water level of 10 cm (Fig. 1). We divided the tank along its long axis into seven equal compartments and placed a Petri dish (diameter 12 cm, height 1.5 cm) filled with gravel (available commercially as aquarium substratum) in the centre of each compartment (Fig. 1). We measured the dimensions of 50 randomly selected gravel particles using ImageJ software. The gravel size, expressed as the means of the two perpendicular axes of the ellipses circumscribed on the particle shapes was 28.2 ± 3.6 mm. Gravel and stone substrata are known to be preferred by *Dikerogammarus* species (Van Riel et al. 2009; Boets et al. 2010) and *P. robustoides* (Jermacz et al. 2015b), thus we used this type substratum to induce a strong competition between them. We did not use other substrata as the three studied species show different preferences towards sand, macrophytes, etc. and this would lead to habitat partitioning and reduction of the competition, as shown by previous studies (Kley and Maier 2005;

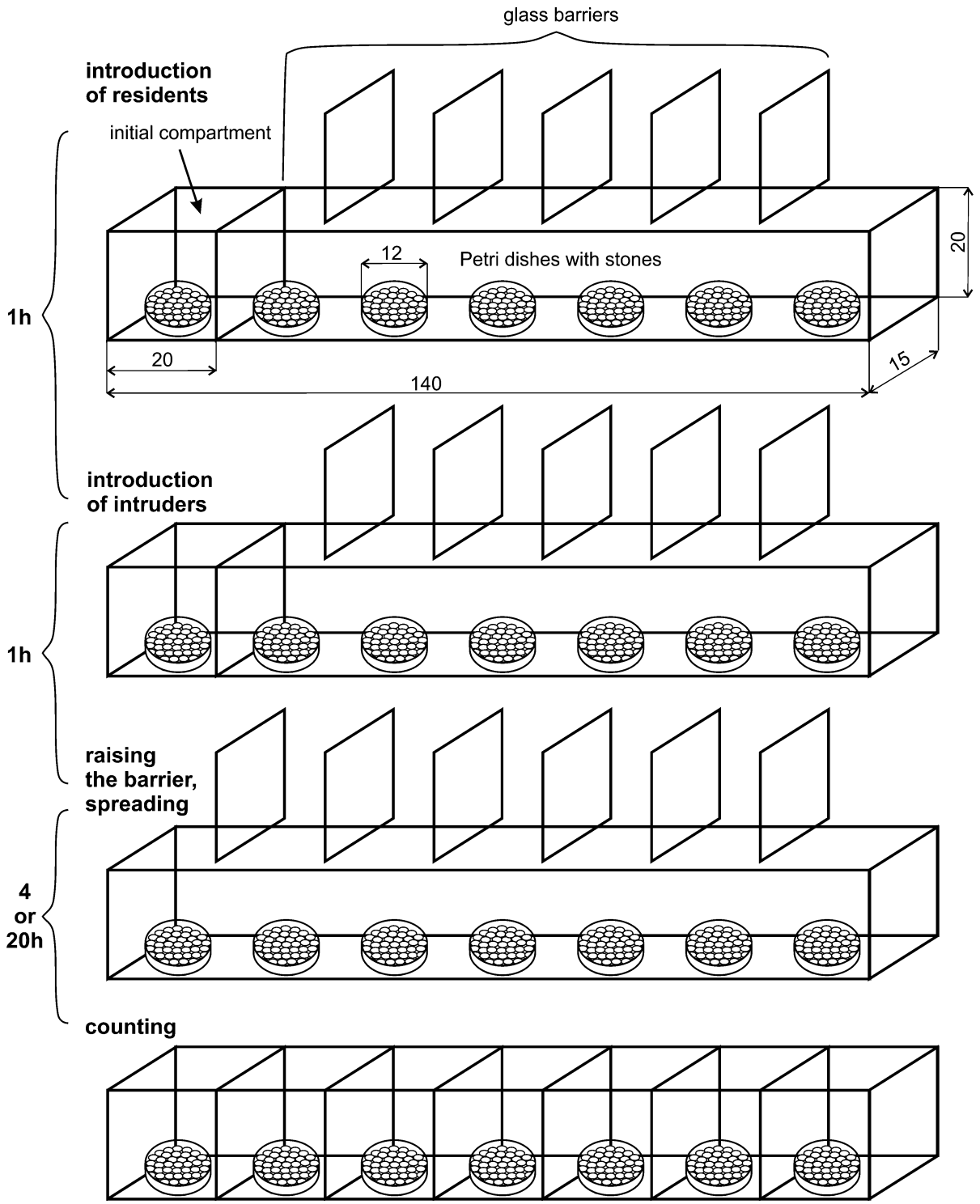


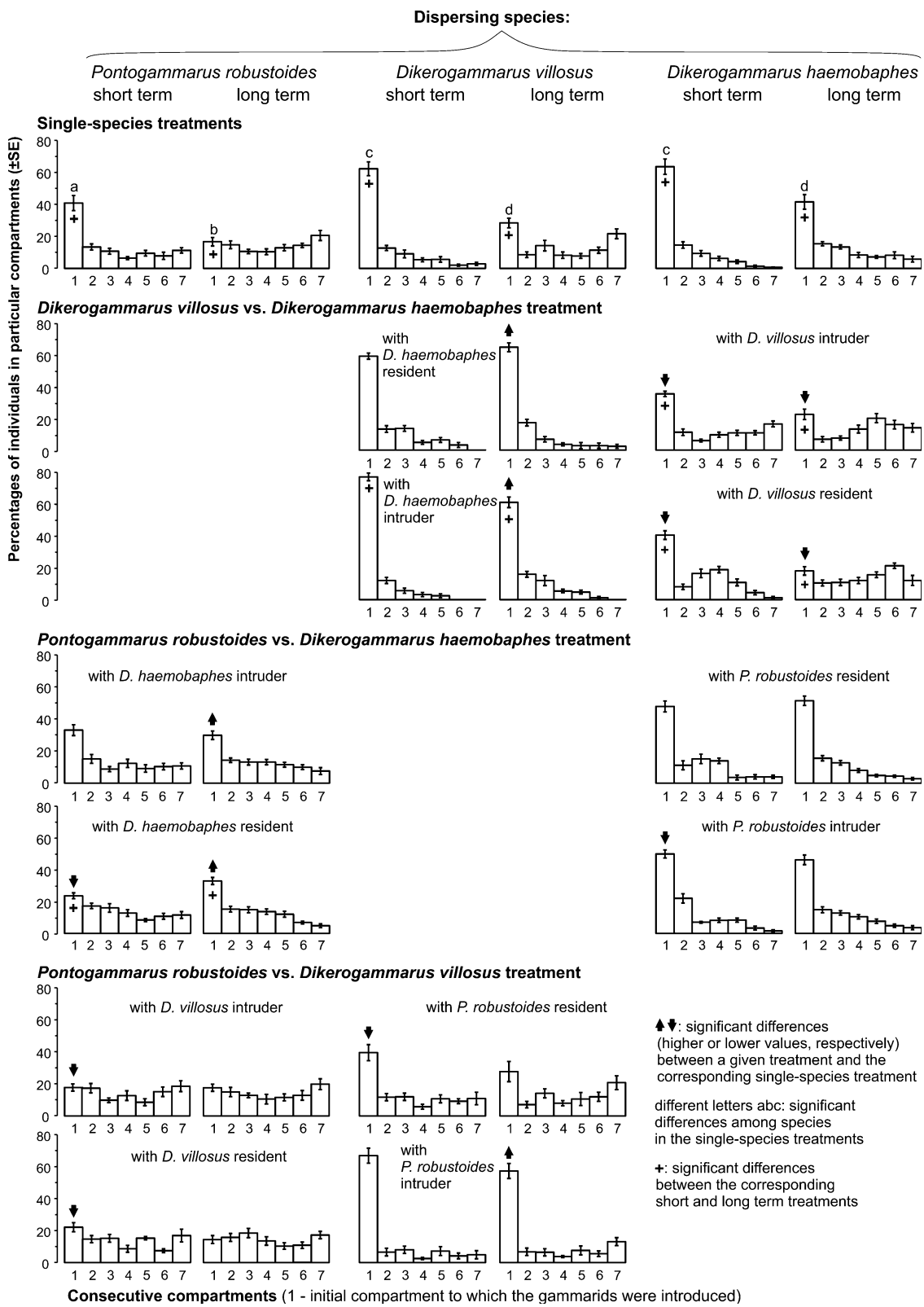
Fig. 1 Experimental tank and design. Dimensions are given in cm

Table 1 Two-way ANOVA of gammarid behaviour

	Dependent variable	Species	Factor	*df*	MS	*F*	*P*
A	% of gammarids in the first compartment	*P. robustoides*, all treatments	Accompanying species	4	0.12	9.87	<0.001
			Exposure time	1	0.09	7.40	0.008
			Interaction	4	0.10	8.00	<0.001
			Error	90	0.01		
		D. villosus, all treatments	Accompanying species	4	0.48	27.48	<0.001
			Exposure time	1	0.52	29.81	<0.001
			Interaction	4	0.11	6.38	<0.001
			Error	90	0.02		
		D. haemobaphes, all treatments	Accompanying species	4	0.32	25.77	<0.001
			Exposure time	1	0.42	33.78	<0.001
			Interaction	4	0.08	6.14	<0.001
			Error	90	0.01		
B	Dispersal index	*P. robustoides*, all treatments	Accompanying species	4	2.41	8.18	<0.001
			Exposure time	1	0.83	2.81	0.097
			Interaction	4	1.76	5.98	<0.001
			Error	90	0.29		
		D. villosus, all treatments	Accompanying species	4	11.17	37.90	<0.001
			Exposure time	1	11.65	39.54	<0.001
			Interaction	4	2.63	8.93	<0.001
			Error	90	0.29		
		D. haemobaphes, all treatments	Accompanying species	4	10.07	48.34	<0.001
			Exposure time	1	8.90	42.72	<0.001
			Interaction	4	1.82	8.72	<0.001
			Error	90	0.21		
C	% of gammarids in the first compartment	All species, single-species treatments	Species	2	0.37	18.58	<0.001
			Exposure time	1	1.23	61.96	<0.001
			Interaction	2	0.02	1.02	0.366
			Error	54	0.02		
D	Dispersal index	All species, single-species treatments	Species	2	8.51	32.52	<0.001
			Exposure time	1	25.26	96.55	<0.001
			Interaction	2	1.09	4.18	0.021
			Error	54	0.26		

Impact of heterospecific gammarids on the behaviour of particular species (A, B) and behavioural differences among species in the single-species treatments (C, D)

Jermacz et al. 2015a). On the other hand, in anthropogenically modified rivers, habitat heterogeneity is greatly impaired (Van Riel et al. 2007; Leuven et al. 2009) and possibilities of spatial segregation among species are lower, which may result in different responses, such as long distance migrations. Therefore, we intended to check gammarid behaviour in a uniform habitat to simulate such conditions.


Dispersing species:
Pontogammarus robustoides
Dikerogammarus villosus
Dikerogammarus haemobaphes
short term
long term
Single-species treatments
Percentages of individuals in particular compartments (±SE)
Dikerogammarus villosus vs. Dikerogammarus haemobaphes treatment
with D. haemobaphes resident
with D. haemobaphes intruder
with D. villosus intruder
with D. villosus resident
Pontogammarus robustoides vs. Dikerogammarus haemobaphes treatment
with D. haemobaphes intruder
with D. haemobaphes resident
with P. robustoides resident
with P. robustoides intruder
Pontogammarus robustoides vs. Dikerogammarus villosus treatment
with D. villosus intruder
with D. villosus resident
with P. robustoides resident
with P. robustoides intruder
: significant differences (higher or lower values, respectively) between a given treatment and the corresponding single-species treatment
different letters abc: significant differences among species in the single-species treatments
+: significant differences between the corresponding short and long term treatments
Consecutive compartments (1 - initial compartment to which the gammarids were introduced)

◀**Fig. 2** Distribution of gammarids in the compartments of the experimental tank in the presence of various competitors. Behavioural responses of particular species are shown in consecutive columns, whereas particular treatments are arranged in the same rows. Accompanying species are indicated on the plots. *Arrows* pointing upwards or downwards indicate that in a particular treatment the percentage of gammarids in the initial compartment was significantly higher or lower (respectively) than in the corresponding control single-species treatment. *Plus* ('+') signs indicate significant differences in gammarid percentages between the corresponding short and long term treatments. *Different letters* (a–c) above the *bars* of the single-species treatments indicate significant differences between the percentages of particular species in the initial compartment

Before the experiment, we separated the outermost compartment of the tank with a glass barrier and introduced 25 gammarid individuals, the "residents", to this compartment. After 1 h, when the residents had established themselves in the substratum, we introduced the next 25 gammarids, the "intruders". The intruders were introduced to the substratum already occupied by the residents and had to outcompete them to take over the most suitable sites within the substratum. One hour is sufficient for gammarids to get used to experimental conditions and find a suitable shelter (Kinzler and Maier 2006). During subsequent manipulations, we observed that most of the individuals in our study were hidden in the substratum after 1 h, which confirms this statement. We removed the barrier after the next 1 h and allowed the gammarids to spread freely all over the tank for 4 h (short-term trials) or 20 h (long-term trials). Finally, we separated all compartments with glass barriers and counted the gammarids (Fig. 1).

We tested all pairwise combinations of gammarid species, replicated 10 times, as well as single-species controls (with the same species used as a resident and intruder). Each individual was used only once in the experiment.

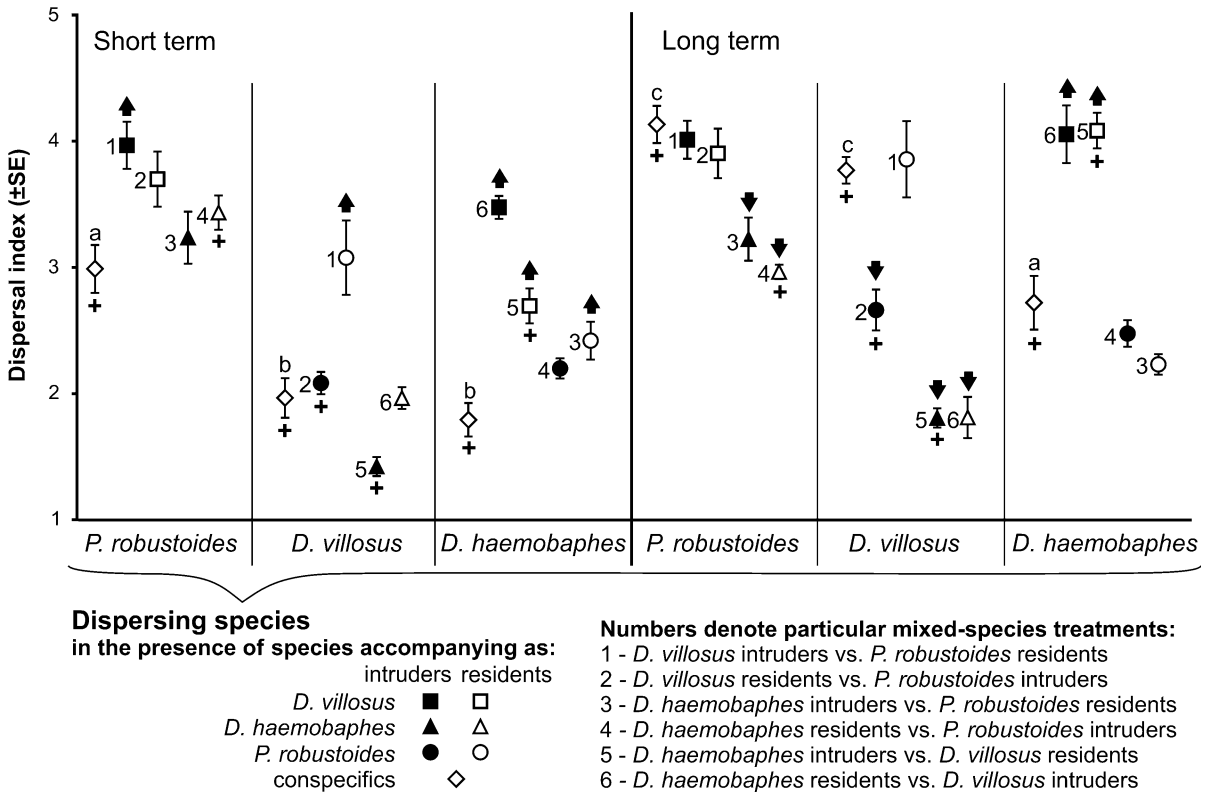


Fig. 3 Dispersal index showing the rate and distance of spread of gammarids from the initial compartment of the experimental tank in the presence of various competitors. *Numbers* 1–6 indicate particular mixed-species treatments. See Fig. 2 for the meanings of other symbols

We conducted the experiments in darkness. Water quality parameters (mean ± SD), monitored with a multimeter Multi340i (WTW GmbH, Weilheim, Germany) were as follows: temperature 20.3 ± 0.66 °C, pH 8.0 ± 0.15, conductivity 472 ± 41.7 µS/cm, oxygen saturation 72.7 ± 8.46 %.

Data analysis

We analysed two dependent variables. The first variable was the percentage of individuals occupying the initial compartment of the tank, which allowed to determine the ability of gammarid species to displace one another from the occupied habitat. The second variable was a dispersal index (DI), calculated as the mean number of compartment occupied by all gammarids in the tank:

$$DI = \sum(N_i * i) / \sum(N_i)$$

where N_i is the number of gammarids in the compartment i and i is the consecutive number of the compartment (1–7, with the number of the initial compartment = 1).

Such an index allowed to analyse the dispersal of gammarids in the entire tank and to distinguish between gammarid displacement to the nearby habitat (compartment) and stimulation of spread over a longer distance.

Percentage data were arcsine square root transformed prior to the analysis. It was not possible to include all the data into a single model because the results of the mixed-species treatments were not independent of each other (both species were together in the tank), whereas those from the single-species treatments could not be paired. Therefore, we conducted separate two-way ANOVAs for each gammarid species to test the effect of (1) Accompanying species (5 variable levels: a single-species control and two other gammarid species used as residents and intruders) and (2) Exposure time (long-term and short-term trials). Moreover, we tested the differences in dispersal among gammarid species using a two-way ANOVA on the data from the single-species trials, with (1) Species (3 levels) and (2) Exposure time as factors. Significant ANOVA effects were followed by sequential-Bonferroni corrected t-tests used as a post hoc procedure.

Results

We did not observe any cases of intra-guild predation during the experiment, collecting the same numbers of individuals as had been introduced to the tanks. Behaviour of all gammarids depended on the accompanying species and exposure time, resulting in significant interactions between these factors in all analyses (Table 1A, B).

After the shorter exposure, individuals of *Pontogammarus robustoides* in the control treatment tended to remain near the place of their introduction. *Dikerogammarus villosus* forced them to move along the experimental tank, irrespective of the order of species introduction (Figs. 2, 3). The short-time effect of *Dikerogammarus haemobaphes* was similar to that of *D. villosus*, though less pronounced and limited only to the resident competitors and to the initial tank compartment (no significant effect for the dispersal index, Fig. 3). After the longer exposure, *P. robustoides* dispersed equally all over the tank in the control treatment and in the presence of *D. villosus*, but the presence of *D. haemobaphes* made them stay near their initial location relatively more often (Figs. 2, 3). Interestingly, the dispersal of *P. robustoides* in the presence of *D. haemobaphes* residents decreased significantly after the longer exposure compared to the short-time treatment, indicating that some individuals might return to the place of introduction after initial spreading (Fig. 2).

Dikerogammarus villosus did not respond to the short-term exposure to the other gammarids except their significant displacement by *P. robustoides* residents (Figs. 2, 3). After the longer exposure, individuals of *D. villosus* significantly decreased their dispersal in the presence of the other species and stayed in the initial compartment more often than in the control treatment.

After the short exposure, *D. haemobaphes* was forced to migrate along the tank by both heterospecific competitors, irrespective of their introduction status (Figs. 2, 3). After the longer time, only the effect of *D. villosus* remained significant.

Gammarid behaviour in the single-species treatments differed significantly among the studied species. Both *Dikerogammarus* species left their initial locations less often than *P. robustoides* at both exposure times, resulting in a significant species effect

in ANOVA (Table 1C). Also, all species were more dispersed after the longer exposure (Figs. 2, 3). However, after the longer exposure, *D. villosus* was distributed in the tank more uniformly than *D. haemobaphes* (Fig. 3), which remained mostly within the first three compartments (Fig. 2). This resulted in a significant species x exposure time interaction in the dispersal index analysis (Table 1D). With regard to this index, the short-term dispersal of *P. robustoides* was greater from that of both *Dikerogammarus* species, whereas after the longer exposure the distribution of *D. haemobaphes* was more limited to a few first tank compartments than that of the other two species (Fig. 3).

Discussion

Gammarids are highly motile organisms, which migrate in response to a number of factors, including food and predator cues (Wisenden et al. 2009), water flow (Dennert et al. 1969) and competitor pressure (Jermacz et al. 2015a). Moreover, their dispersal is influenced by human vectors, including biofouling of artificial surfaces (Martens and Grabow 2008; Davidson et al. 2009), intentional introductions (Arbaciauskas 2002) and overland transport (Bącela-Spychalska et al. 2013; Bącela-Spychalska 2015). In our study, their dispersal rate differed between single-species and mixed-species treatments, which shows that the presence of related species is another factor influencing their movement and microhabitat occupancy. Our results support the hypothesis that, indeed, the weaker species is forced to leave its initial location and disperse more in the experimental tank. *Dikerogammarus villosus*, also called "the killer shrimp", is a very strong competitor (Dick and Platvoet 2000; Van der Velde et al. 2000; Kinzler and Maier 2003; MacNeil et al. 2011), capable of outcompeting other species to less preferable habitats (Van Riel et al. 2007; 2009; Jermacz et al. 2015a). In our experiments, it successfully displaced *D. haemobaphes* in all treatments and *P. robustoides* in the short term treatments. It pushed out the other species even as an intruder, probably due to its aggression and active fighting for a shelter (Dick and Platvoet 2000; Platvoet et al. 2009). *Dikerogammarus villosus* can also eliminate other amphipods by intraguild predation (Kinzler and Maier 2003; MacNeil and Platvoet 2005; Kinzler et al. 2009) but we did not observe any predation in our experiments, so this factor did not affect gammarid dispersal in our study.

The strong competition between two *Dikerogammarus* spp. could result from their similar dispersal habits (shown in single-species trials), facilitating interspecific encounters. Another reason may be a close phylogenetic relationship between them (Cristescu and Hebert 2005). Species from the same genus are more likely to compete with each other than those from different genera, which results in phylogenetic overdispersion, which is the tendency of co-occurring species to be less related with one another than expected by chance (Cooper et al. 2008; Cavender-Bares et al. 2009; Vamosi et al. 2009).

Pontogammarus robustoides also seems effective in shelter guarding, as it did not allow *D. villosus* intruders to settle successfully in the short term treatment. Moreover, it is as predatory as the killer shrimp (Bącela-Spychalska and Van der Velde 2013) and its aggression may also be similar (own observations). On the other hand, in the single-species treatments, *P. robustoides* was more active and "explorative" than *Dikerogammarus* spp. Truhlar and Aldridge (2015) observed that *D. villosus* was also relatively less active and explorative than other gammarids (e.g. *Gammarus pulex*). That is why *P. robustoides* in our study left the initial compartment faster than the other species and therefore its impact on the long-term dispersal of *D. haemobaphes* was lower than that of *D. villosus*. Such a strong tendency for spontaneous dispersal enables *P. robustoides* to test a variety of available microhabitats and finally find a suitable site in a patchy environment. It occurs on a wide range of different substrata, such as macrophytes, tree roots, mussel beds, sand or gravel (Gruszka 1999; Kobak and Żytkowicz 2007), whereas *Dikerogammarus* spp. are limited to large-grain, hard substrata or mussel beds (Boets et al. 2010). Thus, *P. robustoides* seems best adapted to locate new suitable sites in its neighbourhood and can avoid excessive competition by relocation to alternative microhabitats (Jermacz et al. 2015a). However, its long-distance spread is limited by its avoidance of flowing waters (Jażdżewski et al. 2002).

Dikerogammarus villosus and *P. robustoides*, which seem the strongest competitors, in the long

term single-species experiments spread more than in the presence of *D. haemobaphes*. It may be explained by defending local shelters by the stronger species in the presence of heterospecific interactions or by the weaker competition pressure from *D. haemobaphes* compared to that exerted by conspecifics. Interspecific competition is usually weaker than intraspecific competition (Connell 1983), and our results seem to be congruent with that hypothesis, though some exceptions from this rule do exist (Jermacz et al. 2015a).

Microhabitat heterogeneity allows competing species to co-exist when they can partition available space and avoid direct interactions (Hesselschwerdt et al. 2008; Platvoet et al. 2009; Koester and Gergs 2014). In our study, the gammarids could not switch to another microhabitat, but were able to avoid competition by dispersal. This reflects a common situation in highly regulated European rivers with decreased microhabitat diversity (Van Riel et al. 2007; Leuven et al. 2009), where weaker species would spread faster in the presence of stronger competitors. The outcompeted individuals may decline in a new area due to unsuitable local conditions, but their high invasive potential (a set of specific life history traits and wide ecological tolerance; Grabowski et al. 2007a) may allow them to thrive, leading to the faster increase of their range. A larger number of displaced individuals and/or more frequent displacement events would increase the probability of a successful invasion.

In the field, *D. haemobaphes* has often been observed to appear first, whereas *D. villosus* was the latest newcomer in most of the colonised water bodies. The spread of these species in the large part of the central migration corridor (the Dnieper, Prypiat, Bug and Vistula rivers, Bij de Vaate et al. 2002) followed that pattern. *Dikerogammarus villosus* appeared in the Vistula River system at least 4 years after *D. haemobaphes* (Konopacka 1998; Jażdżewski and Konopacka 2002; Jażdżewski et al. 2004; Grabowski et al. 2007b). In the Danube/Rhine river system, the invasion of both species was more simultaneous (Bij de Vaate et al. 2002), but *D. haemobaphes* more often spread to the affluents of the main rivers, whereas its congener was limited to the main rivers (Weinzierl et al. 1996; Kley and Maier 2003; own unpublished data). Such a pattern has usually been explained by the high dispersal rate of *D. haemobaphes*, being a "pioneer" species often colonising upstream the rivers (Jażdżewski 1980). Our results, showing the weak dispersal of *D. haemobaphes* in the single-species treatments, shed new light on the history of invasion of the two *Dikerogammarus* spp., suggesting that competitive displacement may increase the dispersal rate of the weaker competitor and contribute to its fast spread. There, due to its highly invasive character, it can develop fast growing populations and outnumber native species (Jażdżewski et al. 2004; Grabowski et al. 2007a; Bącela-Spychalska and Van der Velde 2013).

A similar mechanism may help explain the invasion pattern of *Echinogammarus ischnus*, which was the first Ponto-Caspian gammarid colonising European inland waters (Jażdżewski 1980; Bij de Vaate et al. 2002). This species is also often outcompeted by later colonisers, such as *D. villosus* (Van Riel et al. 2006) and *P. robustoides* (Żytkowicz and Kobak 2008). Another example of that phenomenon is the case of invasive dreissenid mussels. The quagga mussel *Dreissena rostriformis bugensis* is a stronger competitor, gradually displacing the zebra mussel, *Dreissena polymorpha* when both species co-occur (Orlova et al. 2005), though the latter species is a faster colonizer with a wider range of occurrence in the early stage of invasion (Garton et al. 2013; Matthews et al. 2014).

Similar results of interactions between competitors (De Meester et al. 2014), as well as between intraguild prey and predators (Wang et al. 2013) were listed highlighting that the dispersal may be an efficient strategy leading to avoidance of adverse interactions between species. Interestingly, in most cases of biological invasions the fastest spreading species are regarded as the strongest competitors with the highest invasive potential (Lockwood et al. 2013). That is in contrast to the aforementioned phenomenon of the high dispersal rate exhibited by weaker competitors to decrease competitive pressure. Our results are congruent with the latter hypothesis, showing that negative interactions may promote spread of weaker species into novel areas, and thus contribute to their range extension.

Thus, we demonstrate two different potential mechanisms which may influence the dispersal of Ponto-Caspian gammarid species. *Pontogammarus robustoides* exhibits a natural tendency to explore new locations and spreads spontaneously even when

not affected by heterospecific competitors. *Dikerogammarus haemobaphes*, on the other hand, displays a strong affinity for the inhabited territory, but migrates in response to the presence of stronger competitors. Both these mechanisms lead to similar results: greater probability of appearance of alien species in novel areas, which in consequence increases their ranges and invasive potential. In contrast to these species, active migrations of *D. villosus* seem relatively slower, which may explain its later appearance in many invaded areas.

In accordance with the "invasional meltdown" hypothesis, positive interactions among various alien species facilitate their establishment in newly invaded areas and therefore contribute to the success of biological invasions (Simberloff and von Holle 1999). We demonstrate that negative relationships among invaders may stimulate their spread to novel areas, thus constituting another important factor promoting biological invasions and explaining the sequence of colonization of new locations.

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